SOME LOWER CRETACEOUS TEREBRATELLOIDEA

By ELLIS FREDERIC OWEN

SYNOPSIS

Several Lower Cretaceous species previously described by Walker, Davidson, Meyer and Keeping are revised and referred to *Tamarella* gen. nov. or *Vectella* gen. nov. Serial sections of representative species of these forms are shown for the first time. In addition, two new species of *Rugitela* from the Neocomian of Lincolnshire and Yorkshire are described and related to forms previously recorded from North Germany and France.

INTRODUCTION

Representative genera of the Mesozoic brachiopod family Zeilleriidae have been recorded from the Trias to the Lower Cretaceous but few of the early records have been further investigated, and the Jurassic genus *Zeilleria* has often been quoted from the Neocomian and, more recently, with those of *Aulacothyris* and *Ornithella* by Middlemiss (1959) and Casey (1961), from Aptian and Albian beds of the Lower Greensand. Some of these Cretaceous brachiopods, while possibly belonging to the same families as Jurassic species, have characters which merit generic distinction.

Until the researches of Muir-Wood (1934, 1936) the internal structures of the British Jurassic Terebratelloidea had been known only from dissections or by chance exposure of brachial loops and cardinalia in damaged specimens. Minor differences in loop development had previously escaped critical investigation and no real advance had been made in their further classification. It is not the purpose of this paper to add to or further discuss the classification of the terebratelloid brachiopods. However, a systematic study has been made of some of the Lower Cretaceous species within this suborder together with comparisons of genera already described by Muir-Wood (1934, 1936) and Cooper (1955).

Some of the early Cretaceous terebratelloid species formerly described by Walker (1867, 1868, 1870) from the Lower Greensand of Upware (Cambridgeshire), Brickhill (Buckinghamshire) and Potton (Bedfordshire) have been revised and referred to *Tamarella* gen. nov. Others, which had been broadly interpreted as *Waldheimia*, *Zeilleria*, *Aulacothyris* and *Ornithella* are placed in *Vectella* gen. nov.

Keeping (1883 : 24) suggested a possible line of evolution of some of Walker's species and related them to others described by Morris (1854) and J. de C. Sowerby (1836) from the Lower Greensand of the Isle of Wight. His suggestions were, however, based mainly on a comparison of external morphology, and an examination of the species listed by him has revealed a degree of homoemorphy. Information obtained from transverse serial sections of these forms has now made possible a revision of his ideas regarding their relationships.

In a description of a brachiopod fauna from the Mural Limestone (Middle Albian) of Arizona, Cooper (1955 : 10) referred *Terebratula tamarindus* J. de C. Sowerby to his new genus *Psilothyris*. He figured a series of etched specimens showing (pl. 3) what

he described as precampagiform, terebrataliform and dalliniform stages in the development of the brachial loop of certain specimens. On the same plate, for comparison, he figured the cardinalia without brachial loop of a dissected specimen which he identified as *T. tamarindus* from the Lower Greensand of Faringdon, Berkshire. If, as he suggested, the etched loops of his specimens exhibit dallinoid development stages, then *Psilothyris* would appear to belong with the Dallinidae.

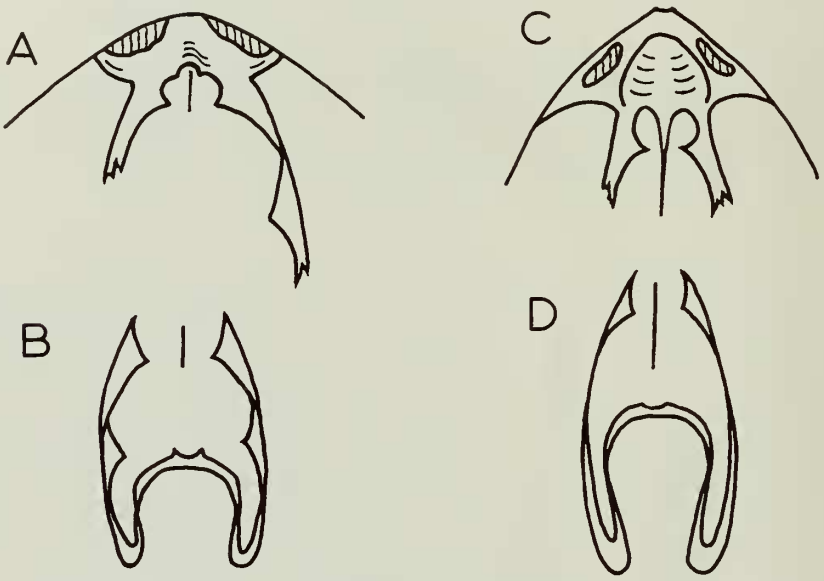

FIG. 1. Diagram illustrating the cardinalia of (A) *Tamarella*, showing the broad hinge-plates with the anterior plication, and (B) a reconstruction of the brachial loop showing the thickening of the descending branches. (C) *Vectella*, showing the deep hinge-trough and long dorsal septum, and (D) reconstruction of the brachial loop.

Although many young specimens of *T. tamarindus* have been examined from the Lower Greensand of Faringdon, Berkshire, no dallinoid stages in loop development have been found, but a remarkable specimen of *T. tamarindus* from Faringdon (Pl. 1, fig. 8*c*) shows what appears to be a thickening of the descending branches some 6 mm. below the dorsal umbo in a brachial valve, 15 mm. long. It is possible that this thickening may be the remains of an early connecting band or attachment. A similar thickening is seen on the descending branches of the brachial loops of specimens of *Psilothyris* figured by Cooper (1955, pl. 3, figs. 18, 19).

The lack of serial sections of the genus *Psilothyris* make absolute comparison with British Upper Aptian species of *Tamarella* impossible and the absence of any evidence of early loop attachment in even very young specimens of *Tamarella* means that any attempt to relate the two genera is purely conjecture. However, the two genera have much in common and it may be necessary at some future date to emend the present study.

The varied brachiopod fauna contained in the condensed Neocomian beds represented in the Claxby Ironstone of Lincolnshire and the Speeton Clay of Yorkshire is

comparable to that described by Roemer (1836–1840) from the Hilsconglomerat of the Hanover district, north-west Germany. Species of zeilleriid brachiopods described as *Terebratula hippopus* and *T. longa* by Roemer are revised here and assigned to the genus *Rugitela* Muir-Wood from the Fuller's Earth Rock of Somerset and said at the time to have a probable range of ? Inferior Oolite to ? Upper Jurassic.

Judd (1868) was the first to recognize Roemer's species *T. hippopus* in Lincolnshire where it occurs fairly abundantly in the Claxby Ironstone. Davidson (1874) erected a varietal name for the British form on the grounds of its larger dimensions, but these are directly proportionate to specimens from the type locality at Berklingen and from Saltzgitter, near Hanover. Furthermore, the pattern of variation in outline, width of shell and depth of dorsal sulcus is identical in both forms and there seems no point in upholding Davidson's varietal name.

SYSTEMATIC DESCRIPTIONS

Family **ZEILLERIIDAE** Allan, 1940

Genus ***VECTELLA*** nov.

DIAGNOSIS. Shell elongate-oval, sulco-carinate to biconvex, rectimarginate to uniplicate or sulcate. Umbo massive, beak suberect. Foramen circular. Beak-ridges sharp, mesothyrid ; interarea short. Test smooth, finely punctate. Deltidial plates conjunct. Short, subparallel dental lamellae embedded in callus ; in mature individuals these lamellae support massive, peg-like, inwardly directed hinge-teeth. Cardinal process poorly developed. Acute septalium forms broad V-shaped hinge-trough supported by short, thick, persistent dorsal median septum. Crural bases triangular, giving rise to zeilleriiform brachial loop developed ventrally.

TYPE SPECIES. *Waldheimia celtica* Morris 1854 : 158.

LOCALITY AND HORIZON. In addition to the type-species, which comes from the Upper Aptian, *Parahoplites nutfieldensis* Zone, Shanklin, Isle of Wight, *Vectella* is represented at an equivalent horizon at Upware (Cambridgeshire) by *V. woodwardi* (Walker) and *V. angusta* (Walker) and by *V. morrisi* (Meyer) from the Bargate Beds of Surrey, from Brickhill (Buckinghamshire) and from Shanklin, Isle of Wight.

REMARKS. *Vectella* is probably a further development of the Jurassic genus *Ornithella* but differs in its more acute septalium and deeper hinge-trough, more acutely triangular hinge-plates and crural bases, and more extensive inner socket-ridges. It differs from *Tamarella* nov. and *Rugitela* in its thicker shell, fused dental lamellae and narrower, anteriorly plane, septalium.

Vectella celtica (Morris)

(Pl. 1, figs. 4*a–c* ; Text-fig. 2)

1847 *Terebratula longa* Roemer ; Davidson & Morris : 255, pl. 19, figs. 1 & 1*a–d*.
1854 *Waldheimia celtica* Morris : 158.
1855 *Waldheimia* (*Terebratula*) *celtica* Morris ; Davidson : 73, pl. 9, figs. 32–35.
1874 *Waldheimia celtica* Morris ; Davidson : 47, pl. 6, fig. 15.

DESCRIPTION. Biconvex, elongate-oval zeilleriid brachiopod, approximately

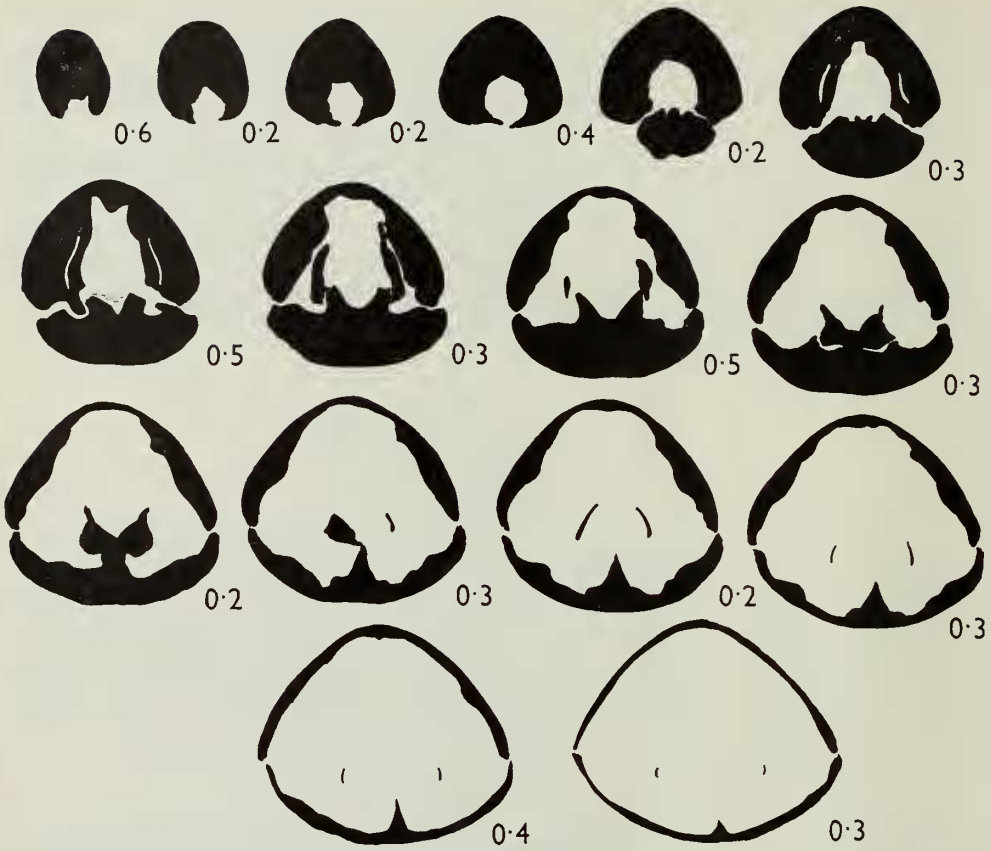

FIG. 2. A series of sixteen transverse sections through the umbonal part of *Vectella celtica* (Morris) from the Upper Aptian, Shanklin, Isle of Wight. BM. B.25801. ×2.

30 mm. long, 19 mm. wide and 18 mm. thick. It has a short, massive umbo, suberect beak and well exposed symphytium. The circular foramen is fairly large with mesothyrid beak-ridges bordering a short interarea. In young forms a marked sulcus is developed posteriorly in the brachial valve and may still be seen in some specimens of mature forms.

LECTOTYPE. Morris was the first to use the specific name *Waldheimia celtica* for a brachiopod from the Lower Greensand of Great Britain and listed it in the second edition of his catalogue (Morris 1854 : 158). He illustrated the species by indicating specimens in Davidson's Cretaceous Monograph which was not, in fact, published until a year later (Davidson 1855 : 73, pl. 9, figs. 32–35). One of these specimens had certainly been taken from a series of four given to Davidson by Morris and now in the Davidson Collection at the British Museum (Natural History), registered number B.6757. The specimens are here regarded as syntypes of *V. celtica* (Morris) and one, figured by Davidson (1855, pl. 9, fig. 33) is chosen as lectotype and has been re-registered BB.42915.

MATERIAL. The lectotype and numerous specimens in the Davidson Collection and general collection of the British Museum (Natural History) from the Upper Aptian, *Parahoplites nutfieldensis* Zone of Shanklin, Isle of Wight, registered as B.6757, B.25800, B.25802–25810. A specimen, B.14728, in the Sedgwick Museum, Cambridge shows the brachial loop and cardinalia in an almost perfect state of preservation.

REMARKS. This species probably illustrates an evolutionary link with some species of the Jurassic genus *Ornithella*. Externally, the long tapering oval outline, massive umbo and carinate pedicle valve suggest such species as *O. ornithocephala* (J. Sowerby) and *O. bathonica* (Rollier). Internally the thickened valve walls and callus embedded dental lamellae in the pedicle valve and the thick septum, supporting short, stout hinge-plates, have much in common with those of *O. bathonica* as shown in transverse serial sections by Muir-Wood (1934 : 544). It can be distinguished from either of the two Jurassic species in its shorter umbo, larger foramen and less acutely tapering valves. It is distinguished from other Lower Cretaceous forms, such as *V. woodwardi* (Walker), by its more regular oval outline, more incurved beak, smaller foramen and absence of anterior sulcation of the brachial valve. It differs from *V. morrisi* (Meyer) in its greater dimensions, stronger biconvexity and lack of uniplication of the anterior margin. It bears a superficial resemblance to *V. angusta* (Walker) from Upware and Brickhill but differs in having a more incurved beak and more robust general outlines. It is nevertheless very near this species.

Vectella angusta (Walker)

(Pl. 1, figs. 5*a–c*)

1868 *Waldheimia mutabilis* var. *angusta* Walker : 400, pl. 19, fig. 5, 5*a*.
1870 *Waldheimia mutabilis* var. *angusta* Walker ; Walker : 562.
1874 *Waldheimia wanklyni* var. *angusta* Walker ; Davidson : 51, pl. 7, figs. 26–28.

DESCRIPTION. Elongate-oval to fusiform *Vectella* about 34 mm. long, 18 mm. wide and 12 mm. thick. Maximum width midway between umbo and anterior margin. Biconvex with acute carination of pedicle valve. Large foramen dominating a slightly produced suberect umbo with wide interarea and well exposed symphitium. Extensive beak-ridges are well defined. Anterior commissure plane.

HOLOTYPE. British Museum (Natural History) no. 67601, figured by Walker (1868, pl. 19, figs. 5, 5*a*) as *Waldheimia mutabilis* var. *augusta*. From the Lower Greensand of Upware, Cambridgeshire.

MATERIAL. In addition to the holotype, eight specimens from Upware, registered no. B.2712 and seventeen specimens from Brickhill, Buckinghamshire, registered no. B.25503, all in the British Museum (Natural History).

REMARKS. As in the case of *Tamarella elliptica* (Walker), this species was originally described as a variety of *Waldheimia mutabilis*, a name already used by Oppel (1861 : 538) for a Liassic species. On Walker's instructions the name *W. wanklyni* was substituted by Davidson (1874 : 51) for *W. mutabilis* Walker.

Walker neither selected nor indicated a type specimen for *W. mutabilis* [= *W. wanklyni*] and the species is, therefore, in doubt. The variety *augusta*, however, is

easily recognizable as a form from the Lower Greensand of Upware and Brickhill. It is in no way related to the species *Tamarella elliptica* and is here promoted to specific rank.

Somewhat resembling *V. celtica* (Morris) in general outline, *V. augusta* differs in less clearly defined features, more acutely convex brachial valve and produced umbo. The form from Brickhill has a shorter umbo and is more regularly elongate-oval in outline than the typical form. It also has a slight depression or sulcus visible on the brachial umbonal region. This depression is more marked in younger specimens.

Vectella woodwardi (Walker)

(Pl. 1, fig. 1*a–c* ; Text-fig. 3)

1867 *Waldheimia woodwardi* Walker ; 455, pl. 19, fig. 3.
1868 *Waldheimia woodwardi* Walker ; Walker : 404.
1874 *Waldheimia woodwardi* Walker ; Davidson : 52, pl. 6, figs. 1–5*a*.
1883 *Waldheimia woodwardi* Walker ; Keeping : 21.

Description. Elongate-oval *Vectella*, about 37 mm. long, 20 mm. wide and 19 mm. thick. The pedicle valve is acutely carinate with steep flanks. It has a short, suberect umbo truncated by a large, circular foramen. Sharp mesothyrid beak-ridges border a short, flat interarea. The finely punctate shell surface is covered by numerous fine growth-lines. A shallow sulcus originating from the umbo in the brachial valve broadens anteriorly. The internal characters are as described for the genus.

Lectotype. The original specimen described and figured by Walker (1867) is one of the two syntypes originally registered with the Walker Collection in the British Museum (Natural History) as 62202. It has been re-registered as BB.42910 and is here selected as lectotype.

Material. Eighteen specimens in the general collection of the British Museum (Natural History) nos. B.25717, B.25801, 62202, BB.21130–38, BB.42922, all from the type locality at Upware, and several internal moulds from Potton.

Remarks. *Vectella woodwardi* is known from the type locality at Upware (Cambridgeshire) and from Potton (Bedfordshire), where it occurs in the *Parahoplites nutfieldensis* Zone of the Upper Aptian. In many respects it resembles *V. celtica* (Morris) which occurs at the same horizon at Shanklin, Isle of Wight but differs in shell convexity and beak characters. These differences in morphology may be due merely to change of environment.

The broad sulcation of the brachial valve in *V. woodwardi* and the shorter, more massive umbo and larger foramen distinguish the species from *V. morrisi* (Meyer) and *V. angusta* (Walker).

Vectella morrisi (Meyer)

(Pl. 1, fig. 7 ; Text-fig. 4)

(Pl. 3, figs. 7–9)

1863 *Terebratula moutoniana* Lankester : 414, pl. 19, figs. 1–3. (non d'Orbigny 1848).
1864 *Waldheimia moutoniana* Lankester ; Meyer : 251, figs. 12–14.
1868 *Waldheimia morrisi* Meyer : 269.
1874 *Waldheimia morrisi* Meyer ; Davidson : 47.

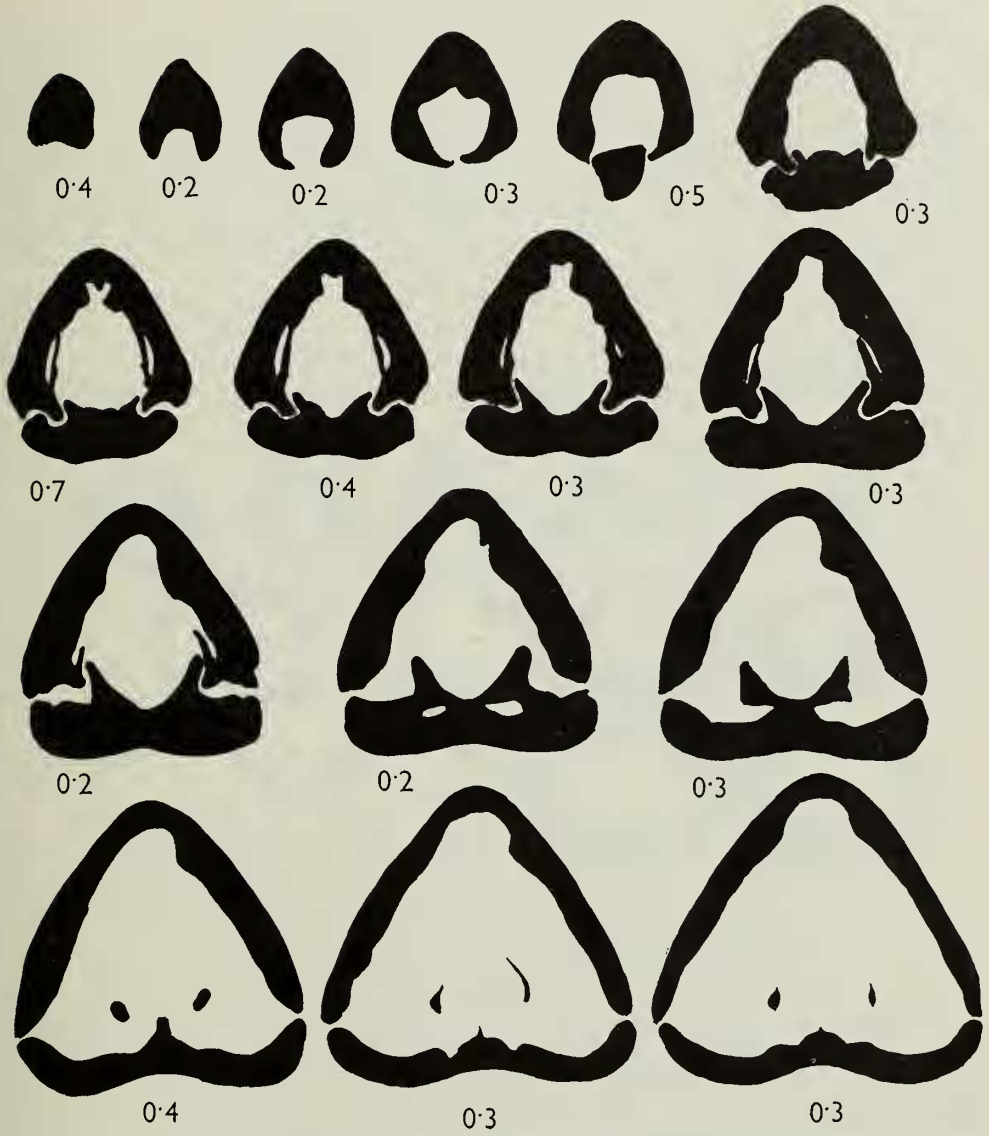

FIG. 3. Sixteen transverse serial sections through the umbo of *Vectella woodwardi* (Walker) from the Upper Aptian, Upware, Cambridgeshire. BM. B.42922. ×2.

DESCRIPTION. Although somewhat terebratulid in general aspect, *Vectella morrisi* is characteristically oval in outline with a shorter, more incurved umbo than other described species of *Vectella*. Both valves are comparatively flat but the brachial valve has a marked median ridge extending two-thirds of the shell length and giving rise to fairly steep flanks. The pedicle valve remains gently convex. The anterior commissure is marked by a faint uniplication distinguishing it from

V. celtica (Morris) which it somewhat resembles. The typical form occurring at Shanklin, Isle of Wight reaches a maximum length of 23 mm., a width of 17 mm. and attains an average thickness of 11 mm.

LECTOTYPE. Meyer (1864 : 249) first described the species as *Terebratula moutoniana* Lancaster and later (1868 : 269) re-described it under the binomen *Waldheimia morrisi* referring to the figured specimens (1864 : figs. 12–14) of his earlier work. Two of the specimens figured by Meyer (figs. 12, 13) were stated to have been collected from the Pebble-bed of Shanklin, while the other (fig. 14) was said to have come from the Pebble-bed of Godalming, Surrey.

These specimens, here regarded as syntypes of *V. morrisi*, are in the Sedgwick Museum, Cambridge and are registered as B.14770–71 and B.16785. The lectotype, here selected, is B.14771. It was originally figured by Meyer (1864, pl. 12, fig. 13) and was collected from the Pebble-bed, *Parahoplites nutfieldensis* Zone, Shanklin, Isle of Wight.

FIG. 4. Fourteen transverse serial sections through the umbo of *Vectella morrisi* (Meyer) from the Upper Aptian, Shanklin, Isle of Wight. BM. B.21937. ×2.

MATERIAL. Apart from the type specimens mentioned above, there are forty-two specimens in the Sedgwick Museum, Cambridge, twenty-nine from Shanklin and thirteen from the Bargate Pebble-bed of Godalming, Surrey, registered B.16838–50, B.14761–69, B.14776–89. Also there are fifty-four specimens in the general collection and Davidson Collection of the British Museum (Natural History) registered B.25506–9, B.6740, B.25815–16, BB.42914, BB.42916–18.

REMARKS. A smaller form of *V. morrisi*, though with similar proportions, occurs in the Bargate Pebble-beds of Surrey and beds of equivalent age at Brickhill, Buckinghamshire. The latter has often been confused with *Tamarella juddi* (Walker) but differs from this species in its more regular oval outline, less acutely convex valves, steeper flanks, shorter umbo, less extensive interarea, rounded beak-ridges and simpler zeilleriform brachial loop. It is approximately 17 mm. long, 11 mm. wide and 8 mm. thick.

Genus *TAMARELLA* nov.

DIAGNOSIS. Shell biconvex. Circular to elongate-oval to pentagonal in outline. Folding rectimarginate to incipiently uniplicate to ligate. Umbo massive, suberect ; beak-ridges sharp. Deltidial plates conjunct. Foramen large, mesothyrid. Shell surface often with marked concentric growth-lines. Median septum short, extending less than one third the length of brachial valve. Septalium broad, shallow, anteriorly arched. Hinge-plates fused, overlapping. Long brachial loop unattached to median septum in adult stage, given off ventrally.

TYPE SPECIES. *Terebratula tamarindus* J. de C. Sowerby 1836.

RANGE. Upper Aptian.

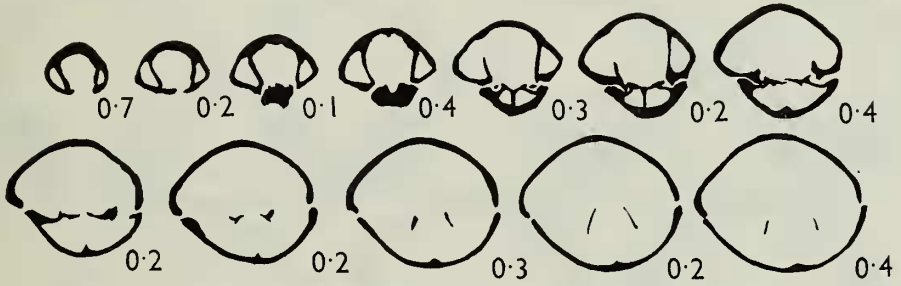

FIG. 5. Twelve transverse serial sections through the umbonal part of *Tamarella tamarindus* (J. de C. Sowerby) from the Upper Aptian, Shanklin, Isle of Wight. BM. B.506. ×2.

Tamarella tamarindus (J. de C. Sowerby)

(Pl. 1, figs. 2*a–c*, 8*a–c*, 10*a–c*, Pl. 3, figs. 5*a–c*, 6*a–c* ; Text-figs. 5, 6)

1836 *Terebratula tamarindus* J. de C. Sowerby : 338, pl. 14, fig. 8.
1843 *Terabratula tamarindus* Sowerby ; Morris : 137.
1855 *Waldheimia tamarindus* (J. de. C. Sowerby), Davidson : 74, pl. 9, figs. 26–31.
1868 *Terebratula tamarindus* var. *magna* Walker : 465, pl. 19, fig. 10.
1874 *Waldheimia tamarindus* var. *magna* (Walker) Davidson : 49, pl. 6, figs. 16–19*a*.
1955 *Psilothyris tamarinda* (Sowerby) Cooper : 14, pl. 3, fig. 25.

DESCRIPTION. *Tamarella* subcircular to elongate-oval in general outline. Acutely biconvex to almost orbicular. Approximately 11 mm. long, 10 mm. wide and 8 mm. thick. The massive umbo is truncated by a large foramen. Well marked mesothyrid beak-ridges border extensive interarea. Shell surface evenly punctate and ornamented by fine concentric growth-lines. The anterior commissure is rectimarginate to incipiently uniplicate. There is sometimes a shallow anterior depression or sulcus bordered by faint carinae noticeable on the pedicle valve. Shell margins show a tendency to gerontic thickening.

NEOTYPE. J. de C. Sowerby *in* Fitton (1836 : 338) described a zeilleriid brachiopod from the Lower Greensand near Hythe, Kent, under the name *Terebratula tamarindus*. No type material was indicated but a specimen, stated to belong to the Sowerby

Collection, was figured (pl. 14, fig. 8) and is now lost. Sowerby's description refers to a specimen with an orbicular outline and with beak-ridges extending some distance down the sides of the valves. The figured specimen appears flattened in lateral profile and with short beak-ridges which are not clearly defined. Although its geo-

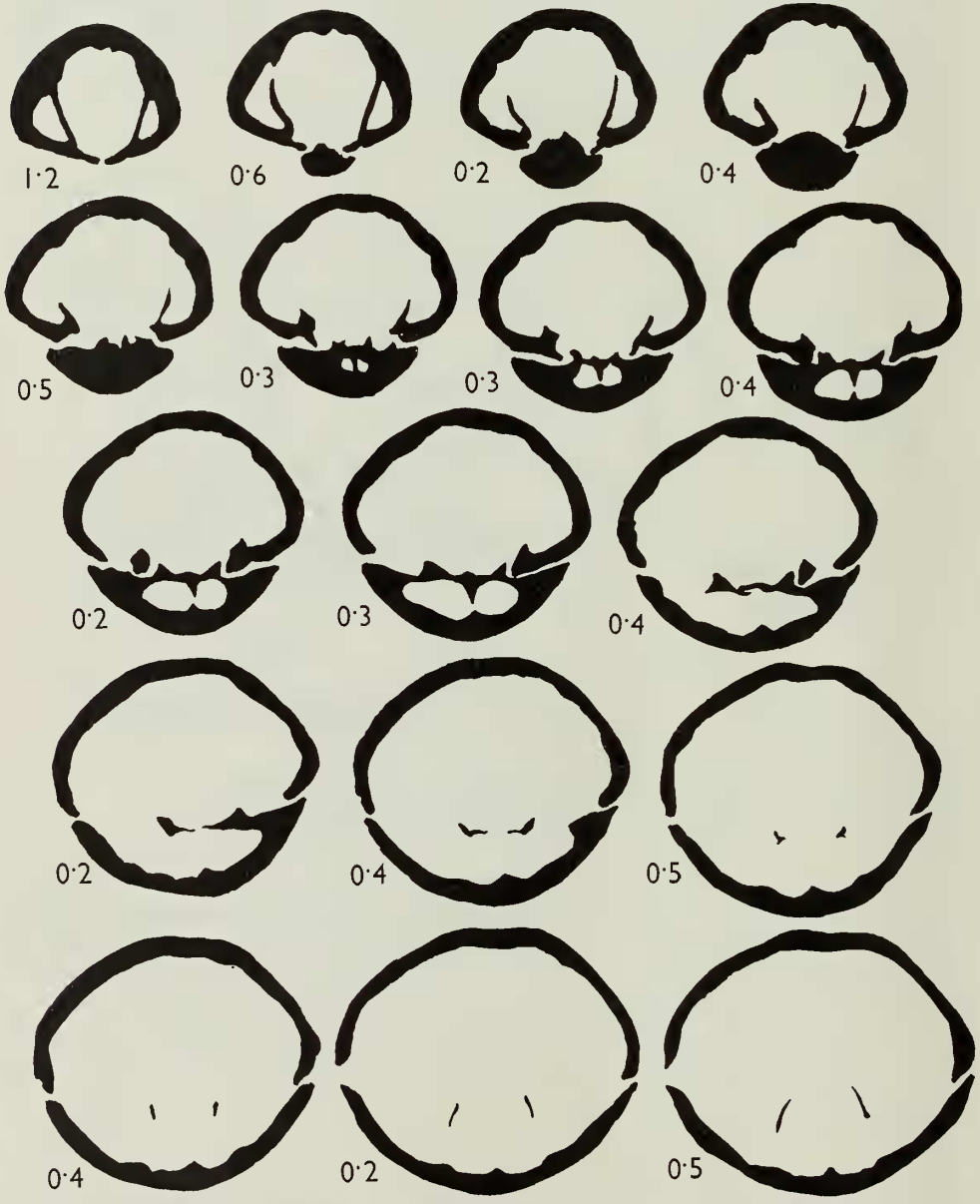

Fig. 6. Seventeen transverse serial sections through the umbo of *Tamarella tamarindus* (J. de C. Sowerby) from the Upper Aptian, Upware, Cambridgeshire. BM. B.25693. ×2.

logical age was stated to be Lower Greensand, no precise beds were mentioned within this horizon nor was any associated fauna listed. Its geological age must, therefore, remain broadly defined. Furthermore, the type locality, said to be "near Hythe, Kent ", although suggesting a Hythe Beds origin, might alternatively have indicated the Sandgate Beds (Upper Aptian) or even an Albian horizon.

The present widely accepted connotation of a brachiopod under the specific name *tamarindus* is Davidson's description (1855 : 74) under the binomen *Waldheimia tamarindus* (J. de C. Sowerby). Davidson figured six specimens from various localities of Lower Greensand age, including one specimen (pl. 9, fig. 26) stated to have been collected from between Hythe and Sandgate, Kent. Unfortunately none of the six specimens figured by Davidson is available in the Davidson Collection and they cannot be traced elsewhere.

Although Sowerby's definition of *Terebratula tamarindus* was vague, the name is so entrenched in literature that it would seem a pity not to preserve it. The preservation of the name, however, depends on the erection of a neotype to replace Sowerby's original figured specimen.

The Lower Greensand includes, among other horizons, the Sandgate Beds (Upper Aptian), which crop out between Hythe and Sandgate, Kent, and from which Sowerby's specimen is likely to have been collected. It is no longer possible to collect brachiopod specimens from the Sandgate Beds exposed in this area but beds of an equivalent age falling within the *Parahoplites nutfieldensis* Zone occur at Shanklin, Isle of Wight and occasionally contain specimens which agree with the original description of *Terebratula tamarindus* J. de C. Sowerby. They also compare favourably with specimens figured by Davidson (1855) from " near Sandgate " and from the Isle of Wight.

A specimen probably used by Davidson (1855 : 74) in his description of the species is figured here (Pl. 3, fig. 5) and proposed as neotype. This specimen, originally registered as B.6724, forms part of the Davidson Collection in the British Museum (Natural History) and was collected from the Upper Aptian beds of Shanklin, Isle of Wight. It has been re-registered as BB.42907.

Material. A further sixty-one specimens of *Tamarella tamarindus* (J. de C. Sowerby), all from the Isle of Wight, are contain in the general collection and the Davidson Collection at the British Museum (Natural History) and are registered as B.506, B.6724, B.25820, B.25187, BB.42905, BB.42906, BB.42919, BB.42920.

Remarks. A larger form of this species approximately 24 mm. long, 21 mm. wide and 15 mm. thick occurs in the Upper Aptian at Upware and Potton. It was originally described and figured as *Terebratula tamarindus* var. *magna* by Walker (1868 : 465, pl. 19, fig. 10) but agrees in every detail with the typical form and has proportionately similar dimensions. *T. tamarindus* is distinguished from other described species of *Tamarella* by its acute biconvexity and almost circular general outline.

Tamarella bonneyi (Keeping)

(Pl. 1, figs. 3*a–c* ; Text-fig. 7)

1883 *Waldheimia bonneyi* Keeping : 129, pl. 7, fig. 4.

Description. Oval to pentagonal, somewhat cinctiform in outline, this species attains an approximate length of 32 mm. with a maximum width of 24 mm. and thickness of 17 mm. Each broad, flattened valve has a shallow anterior sulcation and is ornamented by numerous distinct or clearly defined concentric growth-lines. The umbo is not so produced as in other species of *Tamarella* but shows the same broad, flat interarea bordered by sharp beak-ridges. Although constantly biconvex, the degree of convexity of each valve varies considerably in *T. bonneyi*. Some forms have an almost flat pedicle valve with an acutely convex brachial valve. Others are almost equally biconvex and, apart from their greater length, resemble *T. tamarindus* from Upware.

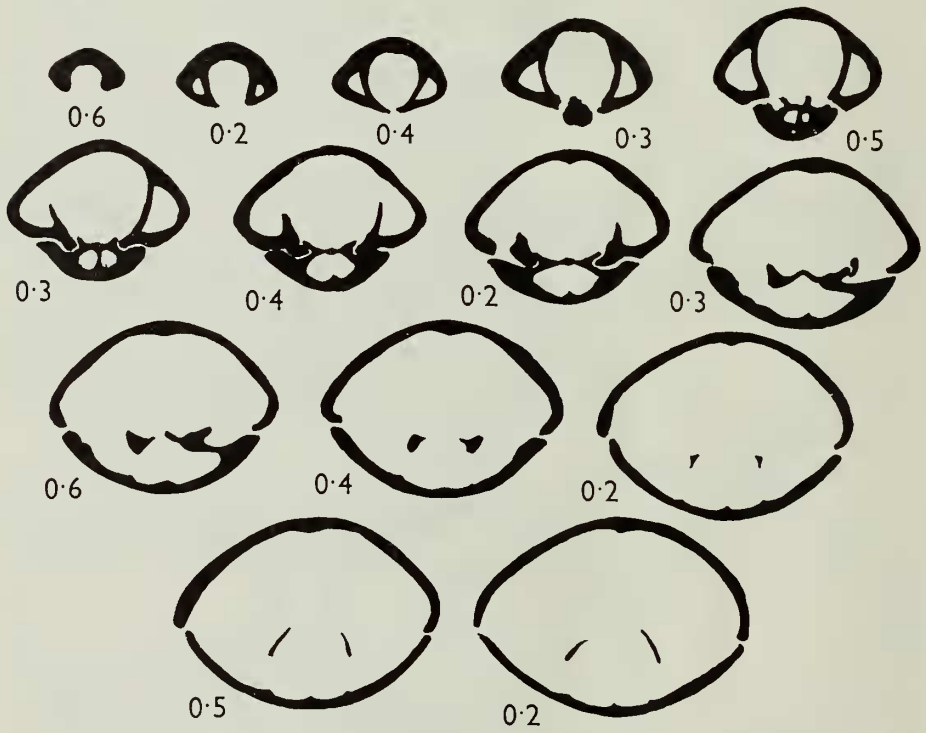

Fig. 7. A series of fourteen transverse serial sections through the umbo of *Tamarella bonneyi* (Keeping) from the Upper Aptian of Brickhill, Buckinghamshire. BM. B.25493. ×2.

Holotype. B.26803 from the Lower Greensand, Upper Aptian of Brickhill, Buckinghamshire in the collections of the Sedgwick Museum, Cambridge.

Material. In addition to the holotype, thirty-eight specimens from Brickhill are in the Sedgwick Museum registered as B.80836–39, B.26509–19, B.25490–513 and thirty-six specimens in the general collections of the British Museum (Natural History) registered as B.25492–93, B.25499.

Remarks. There is a marked similarity between this species and *Tamarella vesta* sp. nov. and attempts have been made to illustrate gradation from one species to

another. A series registered B.25490–531 in the Sedgwick Museum illustrates this variation. *T. bonneyi*, however, appears to be confined to the deposits at Brickhill and *T. vesta* is only rarely found at this locality while it is abundant at Upware.

Tamarella bonneyi is distinguished from *T. vesta* and other species of *Tamarella* mainly by its larger dimensions, broad cinctiform outline and more marked concentric growth-lines.

Tamarella juddi (Walker)

(Pl. 1, figs. 11*a–c*; Text-fig. 8)

1868 *Waldheimia rhomboidea* Walker : 400, pl. 18, figs. 3, 4.
1870 *Waldheimia juddi* Walker : 562.
1874 *Waldheimia juddi* Walker ; Davidson : 50, pl. 7, figs. 15–18.

Description. *Tamarella* about 19 mm. long, 14 mm. wide and 12 mm. thick. Elongate-oval in outline with a maximum width just less than half the distance from the umbo to the anterior margin. Acutely biconvex in lateral profile with marked marginal growth-lines. Short massive umbo and suberect beak with large foramen and sharp mesothyrid beak-ridges. An extensive interarea exposes conjunct deltidial plates. Anterior margin laterally compressed and incipiently uniplicate.

Lectotype. Although the species was originally described by Walker (1868 : 400) as *Waldheimia rhomboidea*, it has never been referred to under this name. Walker mistakenly thought the name to be preoccupied by *Terebratula rhomboidea* Barondi 1855, from the Tertiary of Italy and subsequently changed the name (1870 : 562) to *Waldheimia juddi*. As a junior synonym of *W. rhomboidea*, *W. juddi* has

Fig. 8. Thirteen transverse serial sections through the umbo of *Tamarella juddi* (Walker) from the Upper Aptian of Upware, Cambridgeshire. BM. B.25681. ×2.

since become entrenched in literature as the name of a well known fossil brachiopod and is maintained here. Walker's (1868) original description was accompanied by figures of two specimens from the type locality at Upware which are in the general collections at the British Museum (Natural History) registered as 67602. The larger has been re-registered as BB.42929 and is here selected as lectotype (Pl. 1, figs. 11*a–c*).

Material and locality. In addition to the type material, there are fifty-eight specimens in the British Museum (Natural History) registered as B.25681 and B.25682. Among seven specimens in the Sedgwick Museum from the Upper Aptian of Faringdon, registered as B.18400–06, one specimen, B.18400, shows a well exposed brachial loop and cardinalia which appear to be very similar to Cooper's figure of *Psilothyris* (Cooper 1955, pl. 3, fig. 19). The thickened portion of the descending branches can be clearly seen.

Remarks. *Tamarella juddi* is distinguished from other species of *Tamarella* by its acute biconvexity, extensive interarea, laterally compressed and tapering anterior and smaller foramen.

Tamarella vesta sp. n.

(Pl. 1, figs. 9*a–c* ; Text-fig. 9)

1868 *Waldheimia pseudojurensis* (Leymerie) ; Walker : 405, pl. 18, figs. 8–11.
1874 *Waldheimia pseudojurensis* (Leymerie) : Davidson : 48, pl. 7, figs. 12–14.

Diagnosis. *Tamarella* about 22 mm. long, 15 mm. wide and 10 mm. thick. Shell biconvex, elongate-oval to pentagonal in outline. Anterior commissure plane. Folding ligate. Test smooth with prominent growth-lines. Umbo slightly produced, suberect. Deltidial plates conjunct, well exposed. Beak-ridges sharp.

Description. Although characteristically elongate with steep flanks and slightly produced umbo, the range of variation within this species includes forms which are broader and, in some cases, more inflated than the typical. Marked gerontic thickening of the shell margins tends to accentuate the anterior sulcation of each valve.

The generic characters seen in transverse serial sections (Text-fig. 9) show very clearly the overlapping hinge-plates which appear to be more marked in *T. vesta* than in the type-species *T. tamarindus* (J. de C. Sowerby).

Holotype. This was originally one of four specimens in the Walker Collection, British Museum (Natural History) which were used in Walker's description of the species under the name *Waldheimia pseudojurensis* Leymerie. The holotype was figured by Walker (1868, pl. 18, fig. 8) and was collected from the Upper Aptian of Upware, Cambridgeshire. It has been re-registered as BB.42904.

Material and locality. In addition to the holotype, forty-eight specimens from Upware registered as B.25498, B.25699, B.25701, B.25703. In the Davidson Collection there are nine specimens from Upware registered as B.6754 and three from Brickhill registered as B.6755, all in the British Museum (Natural History).

Remarks. Often confused with *Terebratula pseudojurensis* Leymerie from the Middle Neocomian of Marolles, Aube, France, *Tamarella vesta* nevertheless bears a superficial resemblance to this species. It differs fundamentally in its internal

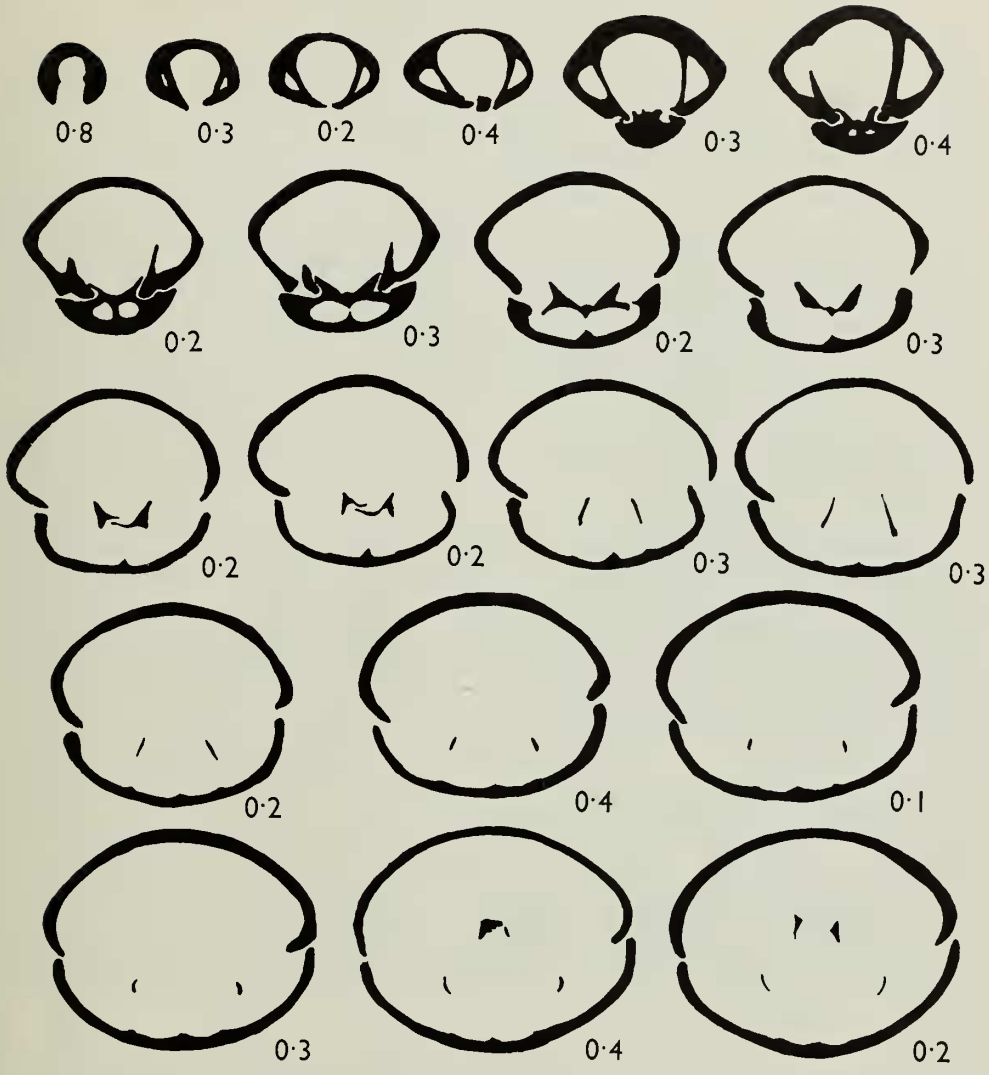

FIG. 9. Twenty transverse serial sections through the umbo of *Tamarella vesta* sp. n. from the Upper Aptian of Upware, Cambridgeshire. BM. B.25700. ×2.

generic characters which can be seen in serial section (Text-fig. 9). It is distinguished from *T. bonneyi* (Keeping) by its more elongate outline, steeper flanks, more produced umbo and less prominent concentric growth-lines. It differs from *T. juddi* and *T. tamarindus* in having flatter or less convex valves and ligate anterior margin.

A common fossil in the Upper Aptian beds of Upware, *T. vesta* occurs, though less commonly, in beds of equivalent age at Brickhill, Buckinghamshire and at Potton, Bedfordshire.

Tamarella elliptica (Walker)

(Pl. 1, figs. 6*a–c*)

1868 *Waldheimia mutabilis* var. *elliptica* Walker : 400, pl. 19, fig. 4.
1870 *Waldheimia mutabilis* var. *elliptica* Walker ; Walker : 562.
1874 *Waldheimia wanklyni* var. *elliptica* Walker ; Davidson : 51, pl. 7, figs. 22–25.

Description. Large oval *Tamarella* approximately 35 mm. long, 26 mm. wide and 15 mm. thick. Both valves are equiconvex and the lateral commissure is almost straight. Somewhat resembling *T. bonneyi* (Keeping) in general outline and convexity, *T. elliptica* lacks the ligation of the anterior margin noted in the former species. A large circular foramen truncates a broad, flattened umbo. Sharp beak-ridges border a fairly extensive interarea. The shell surface is smooth apart from a trace of concentric growth-lines which become more prominent at the margins.

Holotype. In the British Museum (Natural History) registered number 67600, and figured by Walker (1868, pl. 19, fig. 4) as *Waldheimia mutabilis* var. *elliptica*. It was collected from the Upper Aptian of Upware.

Remarks. Walker (1868 : 400) used the name *Waldheimia mutabilis* for a brachiopod from the Lower Greensand of Upware. No specimen was figured nor was any type material indicated. Instead, two forms which Walker called " varieties or sub-species " were erected and named *W. mutabilis elliptica* and *W. mutabilis angusta*. The descriptions of these were accompanied by illustrations (1868, pl. 19, figs. 4, 5) of two specimens now in the British Museum (Natural History) and registered as 67600 and 67601 respectively.

Walker's conception of the species *W. mutabilis* having been established on the description of the two " varieties or sub-species ", is, therefore, indefinable. In any case, the name *Waldheimia mutabilis* had already been used by Oppel (1861) for a zeilleriid brachiopod from the Lower Lias of Germany, and it was for this reason that Walker asked Davidson (1874 : 51) to correct the name to *wankylni* in his Cretaceous monograph.

The varietal name *elliptica* is here raised to specific rank and referred to *Tamarella* gen. nov. The varietal name *angusta* has also been raised to specific rank and referred to *Vectella* gen. nov. on p. 53. Both species are common members of collections of brachiopods from Upware and are easily recognizable.

Genus ***RUGITELA*** Muir-Wood, 1936

Rugitela roemeri sp. n.

(Pl. 2, figs. 1*a–c*, 3*a–c*, 6*a–c*, 8*a–c*, 9*a–c* ; Text-fig. 10)

1836 *Terebratula longa* Roemer : 50, pl. 2, fig. 11.
1839 *Terebratula longa* Roemer ; Roemer : 22, pl. 18, fig. 12.
1840 *Terebratula longa* Roemer ; Roemer : 44, No. 50.
1847 *Terebratula faba* Sowerby ; d'Orbigny : 77, pl. 506, figs. 8, 9, 11, 12.
1864 *Terebratula* (*Waldheimia*) *faba* Sowerby ; Credner : 561, pl. 21, figs. 3, 4, 5.
1868 *Terebratula longa* Roemer ; Quenstedt : 338, pl. 4,6 fig. 99.

Diagnosis. *Rugitela* about 28 mm. long, 18 mm. wide and 14 mm. thick. Shell

biconvex, oval to subtriangular in outline. Umbo short, massive, suberect. Extensive interarea bordered by sharp, mesothyrid beak-ridges. Foramen large, circular. Deltidial plates well exposed, conjunct. Anterior margin rectimarginate to sulcate.

HOLOTYPE. British Museum (Natural History) no. BB.42912, from the Neocomian, Hilsconglomerat of Elligser Brinke, near Hanover, North Germany. According to Judd (1870 : 331) the " Elligser Brinke Schist " has its English equivalent in the *Acanthodiscus speetonensis* Zone at Speeton, Yorkshire and in Lincolnshire.

DESCRIPTION. This species is characteristically elongate-oval in outline with marked growth-lines becoming still more prominent at the margins. Gerontic thickening of the anterior and lateral margins is a common feature. Some variants show a tendency to broad anterior sulcation of the brachial valve.

Internal characters. Short, slightly curved, divergent dental lamellae are embedded in thick callus and support inwardly curving hinge-teeth. Cardinal process not developed. A short septalium develops with long, fused hinge-plates which are deflected ventrally forming a small anterior plication. A long median septum extending two-thirds the length of the shell supports the hinge-plates. Inner and outer socket-ridges are extensive and well marked. Triangular crural bases give rise to thick descending branches of the brachial loop with dorsal development and short crural processes. Fairly broad transverse band developed from ascending branches of the loop. A thickening of the descending branches at a point about one-third the distance from the hinge-plates has been noted in mature forms so far sectioned and may be due to resorption of the attachment branches to the median septum in the dorsal valve. No attachment of brachial loop to septum has been noted in any sections of either young or mature forms.

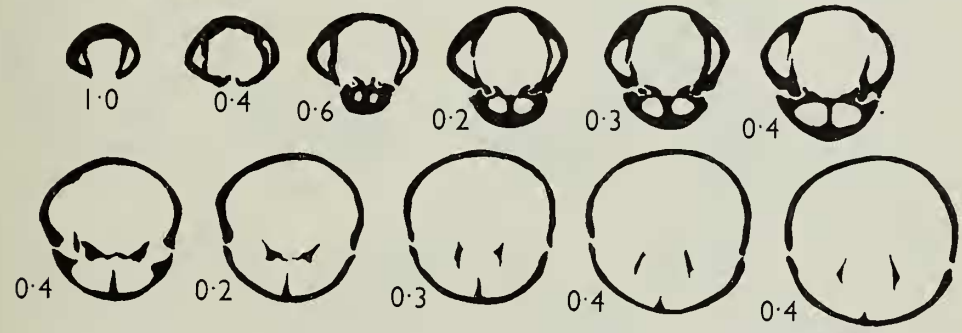

FIG. 10. Eleven transverse serial sections through the umbo of *Rugitela roemeri* sp. n. from the Neocomian of Berklingen, North Germany, showing the characteristic W-shaped hinge-plates and thickened area of the descending branches of the brachial loop. BM. B.35656. ×2.

REMARKS. Zieten (1830 : 52) was the first to use the binomen *Terebratula longa* for a terebratelloid brachiopod which he figured (pl. 39, fig. 7) from the " calcaire jurassique " [Upper Jurassic] of Donzdorf, North Germany. Roemer's description of *Terebratula longa* (1836 : 50, pl. 2, fig. 11) from the Neocomian of Hanover was, therefore, invalid.

D'Orbigny (1847 : 77, pl. 506, figs. 8–12) described and figured a brachiopod from the Neocomian of St. Dizier, Haute Marne, France, and assigned it to *Terebratula faba* Sowerby, a name which J. de C. Sowerby (1836 : 338) had originally used in a description of a brachiopod from the Lower Greensand beds between Folkestone and Sandgate, Kent. Specimens collected from the Lower Albian beds of Folkestone in the Sedgwick Museum (B.17633–17650), have been matched with others collected from the *Leymeriella tardefurcata* Zone of Folkestone by Dr. R. Casey and compare favourably in size, general outline and convexity with *Terebratula faba* as figured by J. de C. Sowerby (1836, pl. 14, fig. 10). A duplicate specimen (Brit. Mus (N.H.) no. B.25994) has been sectioned (Text-fig. 12) and is shown to belong to the genus *Modestella* Owen (1961 : 573) described from the Lower Albian of Folkestone.

D'Orbigny's illustrations (1847, pl. 506, figs. 8–12) were probably an idealization of eight specimens which were collectively numbered 5159 in the d'Orbigny Collection, Laboratoire de Paléontologie, Muséum National d'Histore Naturelle, Paris. Unfortunately only four of these specimens can be traced. One has been identified as a specimen of *Vectella celtica* (Morris) from the Lower Greensand of the Isle of Wight, and another (see Pl. 2, figs. 8*a–c*) is almost identical with the specimen figured by Roemer (1839, pl. 18, fig. 12) from the Neocomian of Hanover.

Rugitela roemeri occurs rarely in Britain, being found in the upper part of the Claxby Ironstone, Lincolnshire and in the Speeton Clay of Yorkshire. A fine, well preserved specimen (Pl. 2, figs. 1*a–c*) from the Claxby Ironstone of Nettleton, Lincolnshire, collected by Mr. Peter Rawson of Hull University, is the only example known from these beds which compares exactly with Roemer's original illustration (1836, pl. 2, fig. 11). The dimensions of this specimen are : 40 mm. long, 20 mm. wide and 16 mm. thick.

A form described here as *Rugitela rugosa* sp. n. resembles *R. roemeri* but is shorter, more gibbous and oval in outline with no marked sulcation of the anterior portion of the brachial valve. It is found in the same beds of the Claxby Ironstone and is probably present in the Speeton Clay, although specimens collected from beds within the range C6 to C3 of Swinnerton (1936–55) and which may belong to this species are too crushed for accurate determination. *R. rugosa* also occurs in the Hauterivian at Salins-les-Bains in the French Jura Mountains. A well preserved example is figured here (Pl. 2, figs. 5*a–d*) for comparison.

The reference of this species to the genus *Rugitela* has been made after careful comparison with transverse serial sections of the type-species *R. bullata* Muir-Wood and extends the range of the genus from ? Inferior Oolite to the Lower Cretaceous. It is possible that the final range may include species from the Inferior Oolite at present under review by Dr. H. M. Muir-Wood.

Material and locality. Well preserved material from the German Neocomian is rare but there are, in addition to the holotype metioned above, nine other specimens in the Davidson Collection, Brit. Mus. (Nat. Hist.) B.6759, BB.41911, from the " Elligser Brinke Schist " of Delligsen near Hanover.

A specimen from the Neocomian of St. Dizier in the Haute-Marne is also in the Davidson Collection (B.6736). It is accompanied by the note in Davidson handwriting which reads : " . . . given to me by d'Orbigny . . . from the d'Orbigny Coll . . . "

Seven specimens, British Museum (Natural History) (BB.42925–31), from the *Acanthodiscus speetonensis* Zone of the Speeton Clay, Yorkshire. Although crushed they compare favourably with the North German forms.

Rugitela rugosa sp. n.

(Pl. 2, figs. 2*a–c*, 4*a–c*, 5*a–c* ; Text-fig. 11)

1874 *Waldheimia faba* d'Orbigny ; Davidson : pl. 6, figs. 12–14.

Diagnosis. Biconvex *Rugitela* about 29 mm. long, 17 mm. wide and 17 mm. thick. Oval to sub-circular in outline. Shell surface covered with pronounced growth-lines. Anterior and lateral margins thickened. Umbo short, slightly incurved. Interarea extensive. Deltidial plates conjunct. Beak-ridges sharp. Anterior commissure, rectimarginate.

Holotype. Davidson Collection, British Museum (Natural History) no. B.6734 from the Claxby Ironstone (Lower Hauterivian) of Acre House, Tealby, Lincolnshire.

Material. In addition to the holotype, four specimens from the Claxby Iron-

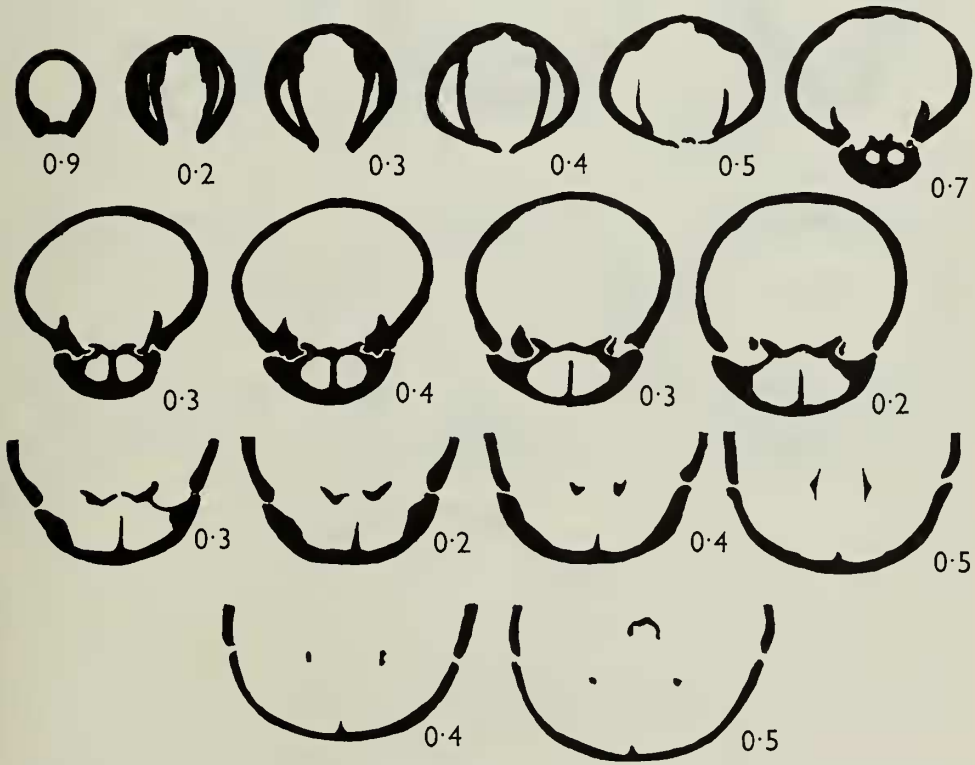

Fig. 11. A series of sixteen transverse sections through the umbonal part of *Rugitela rugosa* sp. n. from the Neocomian, Claxby Ironstone, Acre House, Tealby, Lincolnshire. BM. B.50359. ×2.

stone, British Museum (Natural History) nos. B.6734, B.50358–59, B.50324 and two well preserved specimens from Salins-les-Bains, nos. 33984 and BB.42913. There are two specimens from the Claxby Ironstone in the Sedgwick Museum (B.11400 and B.12278).

Description. In general outline this is a shorter, more gibbous species than

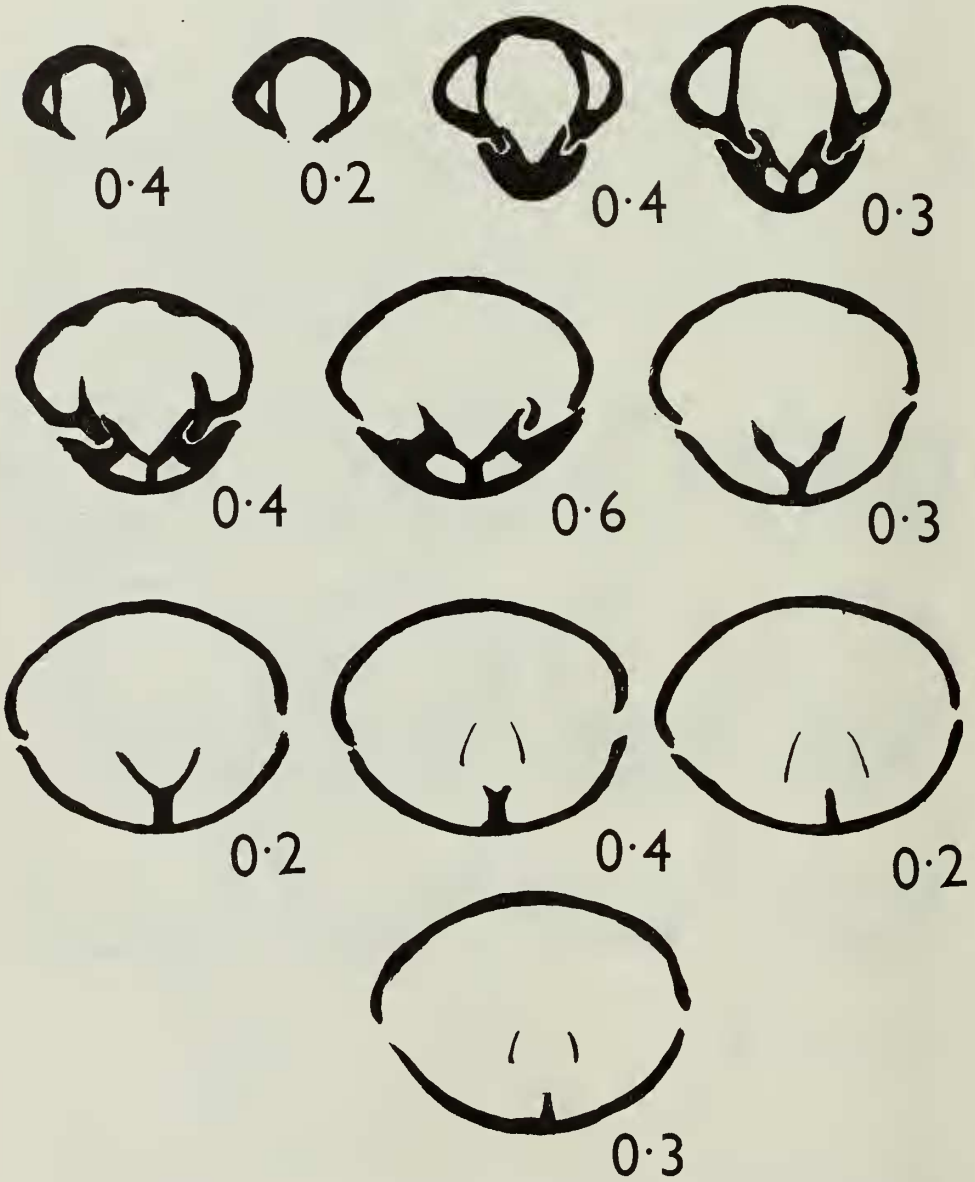

Fig. 12. Eleven transverse serial sections through the umbo of *Modestella faba* (J. de C. Sowerby) from the Lower Albian, Folkestone, Kent. BM. B.25994. ×4.

Rugitela roemeri. It has more acutely convex valves with an absence of any marked sulcation of the brachial valve, although some mature forms exhibit a faint depression in this part of the shell. The surface of the valves is ornamented by numerous concentric growth-lines which give it a rugose appearance. Marginal thickening of the valves is a common feature in more mature forms. The umbo is less produced and more incurved than in *R. roemeri*. Well defined, sharp beak-ridges border an extensive interarea.

Locality and horizon. This species enjoys the same lateral range as *Rugitela roemeri*, occurring in the Lower Hauterivian at Salins-les-Bains in the French Jura Mountains ; a similar horizon at Brunswick, North Germany, and in the Claxby Ironstone of Lincolnshire, as well as the *Acanthodiscus speetonensis* Zone of the Speeton Clay of Yorkshire.

Rugitela hippopus (Roemer)

(Pl. 3, figs. 1*a–c*, 2*a–c*, 3*a–c*, 4*a–c* ; Text-fig. 13)

1840 *Terebratula hippopus* Roemer : 114, pl. 16, fig. 28.
1842 *Terebratula hippopus* Roemer ; Geinitz : 87.
1864 *Terebratula* (*Waldheimia*) *hippopus* Roemer ; Credner : 565, pl. 21, figs. 17, 18, 19.
1866 *Terebratula hippopus* Roemer ; Schloenbach : 33.
1868 *Terebratula ? defluxa* Schloenbach : 31, pl. 2, figs. 10–12.
1868 *Terebratula hippopus* Roemer ; Judd : 245.
1874 *Waldheimia hippopus* ? Roemer var. *tilbyensis* Davidson : 53, pl. 6, figs. 10, 11.
1884 *Terebratula* (*Waldheimia*) *hippopus* Roemer ; Weerth : 62, pl. 11, figs. 5, 6.

Description. This well established species is characterized by its almost circular outline, sulcate brachial valve, slightly incurved beak and acutely carinate pedicle valve. It is 12 mm. long, 10 mm. wide and 8 mm. thick. Because of the similarity of external form it has often been assigned to the Liassic genus.

Aulacothyris. It differs from this genus, however, in having a less elongate outline, smaller dimensions, larger foramen and longer brachial loop.

Internal characters. From the transverse serial section of the species (Text-fig. 13) it is possible to compare the internal characters of *R. hippopus* with sections of species of *Rugitela* figured by Muir-Wood (1936 : 124, 128, 131). While agreeing basically with sections of the type-species *Rugitela bullata* from the Fuller's Earth Rock of Somerset, it appears to have closer morphological affinities with *R. emarginata* from the same horizon and locality.

Neotype. Dr. R. G. Thurrell of H.M. Geological Survey has kindly given me permission to publish some of the notes he prepared in a revision of this species which he included in his thesis for the degree of Ph.D of London University, 1957. The following is a quotation from p. 320 of his thesis :

" Owing to war damage, the Roemer Collection in Hildesheim Museum was partly destroyed. Dr. Friedrich Smid of the German Geological Survey has undertaken to search for the type material, but nothing has so far come to light."

In spite of renewed enquiry no specimens have been forthcoming.

A specimen in the British Museum (Natural History) no. 32313 from the Hilsconglomerat of Berklingen, North Germany (Pl. 3, figs. 2*a–c*) appears to be the only

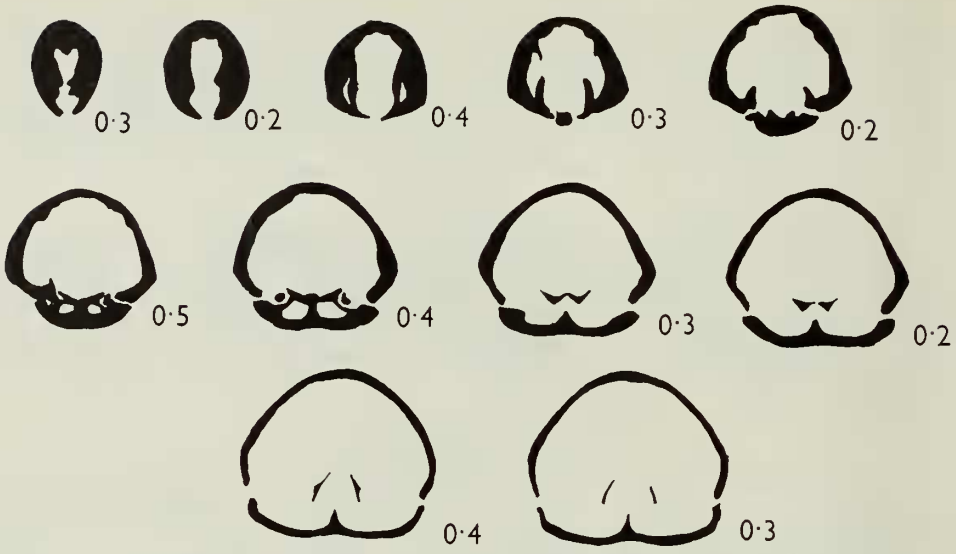

FIG. 13. A series of eleven transverse serial sections through the umbo of *Rugitela hippopus* (Roemer) from the Neocomian, Claxby Ironstone, Acre House, Tealby, Lincolnshire. BM. BB.42934. ×2.

available specimen from the type locality, and is here proposed as neotype. It departs from the original illustration (Roemer 1840, pl. 16, fig. 28) in having less clearly defined beak-ridges and less extensive interarea but, after examination of some 150 specimens from both English and North German localities, these features appear to vary within the species.

MATERIAL AND LOCALITY. Numerous specimens from the Claxby Ironstone from Acre House, Tealby and from Nettleton, Lincolnshire. Ten specimens from the Neocomian of Saltzgitter, Hanover (B.6748, BB.42921, BB.42932), a single specimen from the Speeton Clay of Yorkshire (BB.42923), and one specimen from Marolles, Aube, France (B.6742), all in the British Museum (Natural History).

REMARKS. Differing only in size from the North German form, the British species, originally described as *Waldheimia hippopus* var. *tilbyensis* by Davidson (1874), attains an average length of 15 mm., a width of 13 mm., and a thickness of 10 mm.

The specimen from the Lower Hauterivian of Marolles, France, differs slightly in beak characters. It has less prominent beak-ridges and less extensive interarea.

CONCLUSION

Owing to the lack of recent exposures of the Lower Greensand at Upware, Brickhill and Potton, it is impossible to draw any real conclusions about the distribution of species. All information regarding these localities has been obtained from research on museum collections and the results recorded here.

Critical examination of transverse serial sections of species of *Tamarella* gen. nov. has revealed that they have many characters in common with those of *Rugitela*. For example, the divergent dental lamellae, broad, shallow septalium, anteriorly

arched and fused hinge-plates, triangular crural bases and thickened portion of the descending branches of the brachial loop. The dorsal median septum of *Rugitela* is, however, more strongly developed and considerably longer than that of *Tamarella*.

Prozorovskaya (1962 : 111) described *Gusarella* from the Upper Jurassic of Turkmenistan as a subgenus of *Zeilleria*. Serial sections of the type species *Z.* (*Gusarella*) *gusarensis* have much in common with those of *Tamarella* particularly *T. bonneyi* (Text-fig. 7). The hinge-plates show the anterior arching or plication, and the crural bases, brachial loop and general outline are similar to those of *Tamarella*. In *Gusarella*, however, the dorsal median septum appears to be absent.

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